

48. The Distribution of Secondary Sexual Characters amongst Birds, with relation to their Liability to the Attack of Enemies. By J. C. MOTTRAM, M.B. (Lond.)*.

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INDEX.		Page
MORPHOLOGY :		
Secondary sexual characters. Distribution among birds ...		663
ETHOLOGY :		
Secondary sexual characters. Relation to enemies.....		663
GEOGRAPHICAL :		
Secondary sexual characters. Insular and continental		671

This paper endeavours to show that there is a correlation between extra-sexual dimorphism among birds and their vulnerability to enemies. No attempt is made to account for this correlation. However, in the light of this correlation, the more important theories which have been put forward to account for the presence of secondary sexual characters are briefly considered.

Collection of Material.

In collecting material for classification, works were selected in which many facts were collected on broad lines and with no particular object in view. References are given for all the material used. The work from which by far the most material was taken is 'The World's Birds,' by F. Finn. This is a small volume, in which the families are briefly described in a systematic manner under the headings—diagnosis, size, form, plumage, young, nest, eggs, incubation, courtship, food, gait, flight, notes, disposition and habits, economic qualities, captivity and distribution. A wealth of reliable information is here laid down in a condensed manner, and is, therefore, at once available for classification.

Apart from this work, descriptive monographs have been chiefly consulted. Only families containing more than ten species are considered, as it was thought that a lesser number could not give a reliable picture of the characters of a family.

In order to escape any misunderstanding, the factors to be correlated must first be clearly defined. A species is said to show extra-sexual dimorphism when there is a difference between the somatic characters of male and female. Attention is usually directed to differences in form and colour, but it must be remembered that almost any character may show a difference. It is by no means uncommon to find birds in which the form and colouring of the sexes are identical, but it is quite rare to observe birds

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the males and females of which are entirely alike in every respect apart from their sexual and reproductive organs. Many, in describing the Song-Thrush, remark "sexes alike," forgetting the male's song; nevertheless, it is necessary in a consideration of this kind to accept the classifications of others.

Vulnerability to enemies is essentially a relative term. Unfortunately a classification of birds according to their vulnerability to enemies has not been found. It follows that this subject must be considered in detail.

Birds are subject to attack from the air by hawks, whilst feeding in trees from carnivorous mammals and reptiles, and when on the ground from all three. It follows that birds entirely aerial are more free from enemies than are arboreal or terrestrial ones, and birds entirely arboreal more free than terrestrial. All birds, with very few exceptions, are to some extent aerial. Sea-birds must be almost as free from enemies as aerial birds, as there is little evidence that they are preyed upon by any aquatic animals; and of sea-birds, the oceanic ones must be especially free from enemies, as hawks are not found far from land. The following table, compiled from Finn's 'World's Birds' (see Table I.), sets out the families from this point of view, and shows that birds relatively free from enemies present little sexual difference, whereas those presenting great sexual differences are only to be found amongst terrestrial and arboreal birds.

TABLE I.

	<i>Terrestrial.</i>	<i>Arboreal.</i>	<i>Aerial.</i>	<i>Aquatic.</i>	<i>Oceanic and Maritime.</i>
1. No sex difference ... }	38% 8 [35% ₀]	25% 4 [17% ₀]	50% 4 [17% ₀]	100% 2 [9% ₀]	83% 5 [22% ₀]
2. Usually no sex difference }	24% 5 [33% ₀]	31% 5 [33% ₀]	50% 4 [27% ₀]	—	16% 1 [7% ₀]
3. Sometimes sex difference }	9% 2 [40% ₀]	19% 3 [60% ₀]	—	—	—
4. Usually sex difference ... }	29% 6 [60% ₀]	25% 4 [40% ₀]	—	—	—

NOTES.—Compiled from F. Finn's 'The World's Birds.'

2=Usually no sex difference, and includes the following descriptions:—"Hardly ever a sex difference," "seldom a sex difference," "very slight or no sex difference," "small sex difference," "little s.d.," "rare s.d.," "oftenest alike," "usually small s.d."

4=Usually sex difference, and includes the following descriptions:—"Sexes different," "often sex difference."

The above method of classifying secondary sex characters is used throughout the paper.

(Continued at foot of next page.)

The subject may be approached from other points of view. Many birds are more or less free from enemies on account of possessing powerful weapons of defence—either beaks, talons, wings (*e. g.*, swans), or legs (*e. g.*, cassowaries). Sexual dimorphism should be less commonly found among these birds than among birds in general; and such is the case, as shown in Table II., only hornbills and toucans being to some extent

TABLE II.

	No defensive weapons.	With defensive weapons.
1. No sex difference	38% 11	52% 11
2. Usually no sex difference ...	24% 7	38% 8
3. Sometimes sex difference ...	10% 3	10% 2 { Toucans & Hornbills.
4. Usually sex difference	28% 8	— 0

NOTES.—Compiled from F. Finn's 'The World's Birds.'

Secondary sex characters classified as before.

Reference Nos. :—1 no def. 4, 8, 22, 25, 28, 29, 30, 32, 40, 45, 46 : 2 no def. 10, 26, 31, 37, 39, 42, 44 : 3 no def. 11, 21, 38 : 4 no def. 5, 14, 16, 19, 24, 34, 41, 49 : 1 def. 1, 2, 6, 9, 13, 17, 18, 35, 36, 43, 48 : 2 def. 3, 7, 12, 15, 20, 27, 38, 50 : 3 def. 23, 47.

exceptional. On referring to Table III., it can be seen that these two families have been correctly described as exhibiting "sometimes sex difference," especially in the case of hornbills. As regards toucans, it can be seen that it is chiefly among the smaller and therefore less powerful species that sex dimorphism is found. This, however, is not the case in the hornbills. Although their bills are apparently very powerful, it is doubtful whether they are so in practice; keepers are of opinion that

Notes to Table I., *continued.*

In a few cases birds have been placed in two columns, *e. g.* Pigeons in Terrestrial and Arboreal, Passerine Birds ditto, Divers in Aquatic and Maritime.

Ducks have been placed under Terrestrial, as they are especially liable to the attacks of carnivorous mammals whilst feeding on dry land or in shallow water; they are considered in detail elsewhere.

The bracketed percentages refer to the horizontal lines, the unenclosed percentages to the vertical columns.

Reference numbers for Table I. :—

1 Terr. 6, 8, 9, 25, 29, 43, 45, 46 : 2 Terr. 20, 37, 39, 42, 33 : 3 Terr. 11, 23 : 4 Terr. 34, 5, 14, 16, 19, 41 : 1 Arb. 4, 28, 30, 48 : 2 Arb. 3, 26, 33, 37, 50 : 3 Arb. 23, 38, 47 : 4 Arb. 24, 49, 34, 16 : 1 Aer. 1, 4, 12, 32 : 2 Aer. 15, 31, 40, 44 : 1 Aq. 13, 17 : 1 Ocea. 2, 13, 18, 35, 36 : 2 Ocea. 7 : Nos. 10, 21, 22, 27 omitted.

These numbers refer to the list of birds at the end of the paper, and show how they are distributed in the table; they enable others to criticise the distribution.

a severe bite can only be given when the finger is seized far back in the bill: at the tip the leverage against the jaw-muscles must be very great, and, unlike most long bills, they are unsuitable for stabbing.

TABLE III.

	a.	v.sl.d.	sl.d.	so.d.	d.	
No. of species	18	7	3	3	11	} Hornbills.
Average wing-length..	12.5	15.4	10.8	11.5	15.1	
No. of species	24	6	2	1	6	} Toucans.
Average total length..	18.3	17	14.5	13.5	13	

NOTES.—Compiled from Monographs on the Bucerotidæ by D. G. Elliot and the Ramphastidæ by J. Gould.

a.=sexes alike; v.sl.d.=sexes very slightly different; sl.d.=slightly different; so.d.=some difference; d.=different; v.d. (used in other tables)=very different.

If, instead of considering birds from the point of view of defence we classify them according to their offensive powers, the same conclusion results. Offensive powers are divided according as to whether the birds' diet consists of vertebrates, small vertebrates, invertebrates, or vegetable matter, as set out in Table III. a.

TABLE III. a. (Food of Birds.)

	Food consisting of:—		
	Vertebrates.	Small Vertebrates and Invertebrates.	Small Vertebrates, Invertebrates, and Vegetables.
1	8	7	8
2	4	3	7
3	—	2	3
4	—	—	8

NOTES.—Compiled from F. Finn's 'The World's Birds.'

Numbers at column headings refer to secondary sex characters as before.

Reference Nos.:—1 vert. 1, 2, 13, 18, 32, 35, 36, 43; 2 vert. 7, 12, 20, 27; 1 vert. & invert. 4, 8, 22, 25, 40, 44, 45; 2 vert. & invert. 15, 26, 31; 3 vert. & invert. 21, 28; 1 vert. & veg. 6, 9, 17, 28, 29, 30, 46, 48; 2 vert. & veg. 3, 10, 33, 37, 39, 42, 50; 3 vert. & veg. 11, 23, 47; 4 vert. & veg. 5, 14, 16, 19, 24, 34, 41, 49.

Further, certain birds for other reasons are especially free from enemies. Diving-birds have always a safe refuge at hand,

and should, therefore, present little secondary sexual differentiation. This is shown to be the case in Table IV. In this

TABLE IV.

	Diving Birds.	Non-diving Birds.
1	4 66 ⁰ / ₁₀₀	18 42 ⁰ / ₁₀₀
2	1 17 ⁰ / ₁₀₀	14 32 ⁰ / ₁₀₀
3	0 —	5 12 ⁰ / ₁₀₀
4	1 17 ⁰ / ₁₀₀ (Ducks)	7 14 ⁰ / ₁₀₀

NOTES.—Compiled from F. Finn's 'The World's Birds.'

Sexual classification as before.

Reference Nos. :—1 Div. 3, 13, 17, 35 : 2 Div. 7 : 4 Div. 14 : 1 Non-div. 1, 4, 6, 8, 9, 18, 22, 25, 28, 29, 30, 32, 36, 40, 43, 45, 46, 48 : 2 Non-div. 3, 10, 12, 15, 20, 26, 27, 31, 33, 37, 39, 42, 44, 50 : 3 Non-div. 11, 21, 23, 38, 47 : 4 Non-div. 5, 16, 19, 24, 34, 41, 49.

table ducks form an exception—for, though capable of diving, they often present sex dimorphism. In a previous table they were placed with difficulty, so that it is necessary to study them in more detail (see Table V.). This table shows that the diving-

TABLE V.

Diving Ducks.					Non-diving Ducks.				
a.	v.sl.d.	sl.d.	d.	v.d.	a.	v.sl.d.	sl.d.	d.	v.d.
—	2	3	3	7	—	—	—	—	10

NOTES.—Compiled from J. Gould's 'Birds of Europe,' vol. v.

Swans, Geese, and Sheldrakes, presenting little or no sex difference, were omitted.

The following list shows the placing of the ducks in the above table :—

Div. v.sl.d. *Fuligula leucophthalmos*, *Undina leucocephala* : Div. sl.d. *F. cristata*, *Oidemia fusca*, *O. nigra* : Div. d. *F. ferina*, *F. rufina*, *Mergus albellus* : Div. v.d. *F. marila*, *Clangula vulgaris*, *C. histrionica*, *Harelda glacialis*, *M. merganser*, *M. serrator*, *M. cucullatus* : Non-div. v.d. *Mareca penelope*, *Spatula clypeata*, *Anas boschas*, *Querquedula crecca*, *Q. gloeitans*, *Q. circia*, *Dafila caudacuta*, *Chauliodes strepera*, *Somateria mollissima*, *S. spectabilis*.

habit is associated with a reduction in the amount of secondary sexual difference. No doubt, had a larger amount of material been examined, exceptions would have been encountered; for instance, in the Spot-bill (*Anas pœcilorhyncha*) the sexes are

alike, and perhaps the duck might be considered to be a non-diver, but E. C. Stuart Baker in 'Indian Ducks' says "it is a most expert diver."

The Marbled Duck (*Marmaronetta angustirostris*) forms a like exception, but has unusual habits, which to a large extent protect it from enemies. It never goes ashore; it remains nearly always in rushes. The Andaman Teal (*Nettion albigulare*) is another, but this bird is an insular species and is said to be entirely nocturnal.

However, examples more difficult to account for are to be found; for instance, the Whistling Ducks (*Dendrocygna*). These birds have arboreal habits, and at a sign of danger take to the trees. On the whole, therefore, although at first sight apparently serious exceptions, on more detailed examination ducks are found to fall into line with the rule that diving-birds exhibit less secondary sexual differences than non-divers.

Very few, if any, birds can entirely escape from hawks by means of rapid flight (arboreal birds are to some extent free from their attacks). Two of the favourite quarries of the Eastern hawkers are teal and sand-grouse, among the most rapid fliers. There are, however, a few birds which are able by means of skilful dodging to evade the attacks of hawks—for instance, the hoopoe, of which Finn says "it is easily able to escape from hawks."

TABLE VI.

	Birds mentioned as forming food for man.	No note <i>re</i> edibility.
1	44 0/10 12	43 0/10 10
2	22 0/10 6	39 0/10 9
3	11 0/10 3	9 0/10 2 (Puff-birds and Honey-Guides).
4	22 0/10 6	9 0/10 2 (Trogons and Humming-birds).

NOTES.—Compiled from F. Finn's 'The World's Birds.'

Honey-Guides are not eaten by natives because they are useful in guiding them to honey; Humming-birds possibly because of their small size. Puff-birds are doubtfully described as presenting "sometimes sexual differences," as shown in the following table compiled from P. L. Selater's 'Bucconidae':—

	?	a.	s.l.d.
Puff-birds	33	8	2

?=no note made as to whether sexes are different or not.

As regards Trogons, other works have been consulted but with no result.

Reference Nos.:—1 edib. 2, 9, 22, 25, 29, 30, 32, 35, 36, 43, 45, 46; 2 edib. 7, 20, 33, 37, 39, 42; 3 edib. 11, 23, 47; 4 edib. 5, 14, 16, 19, 34, 41; 1 non-edib. 1, 4, 6, 8, 13, 17, 18, 28, 40, 48; 2 non-edib. 3, 10, 12, 15, 26, 27, 31, 44, 50; 3 non-edib. 21, 28; 4 non-edib. 24, 49.

Birds may avoid enemies in other ways; there is little doubt but that ill-flavour plays a part. Under the heading "Economic Qualities," Finn, in the 'World's Birds,' mentions those birds which form food for man, and this to some extent will separate the well-flavoured from the ill-flavoured. This material is set out in Table VI., which shows that secondary sexual dimorphism is especially to be found among table-birds.

Birds may also be said to avoid enemies by protective coloration. However, it is not possible to examine this aspect statistically, because protective coloration often forms a part of sex dimorphism, the female presenting this coloration and the male not doing so. This is in itself, however, evidence that sex dimorphism is in some way related to enemies.

Size.—Upon size must depend to some extent a species' vulnerability to enemies. Large birds are only open to the attack of large carnivorous animals, whereas small birds are preyed upon by both small and large. Large birds should, therefore, show less secondary sexual dimorphism than medium-sized birds, and these less than birds of small size. Finn describes the size of birds by comparing them with well-known English ones—for instance, of parrots he says "less than tit to that of an ordinary fowl," of hornbills "from that of a hen turkey to that of a pigeon." Birds thus used in description may be classified into large, medium, and small, and, with this as a measure, Table VII. has been compiled. Parrots would fall, therefore, into all three columns, and hornbills into medium and large.

TABLE VII.

	Large.	Medium-sized.	Small.
1	55% 11	43% 18	33% 11
2	20% 4	31% 13	42% 14
3	10% 2	10% 4	9% 3
4	15% 3	17% 7	15% 5

NOTES.—Compiled from F. Finn's 'The World's Birds.'

Table of measure for classification:—Large=swan, goose, turkey, "upwards," heron, 3 ft. and above in length: Medium=jay, dove, raven, rook, mallard, partridge, crow, fowl, pheasant, "medium size," pigeon, jackdaw, hen, duck: Small=lark, "very small," thrush, sparrow, blackbird, tit, swallow, quail, starling, linnet, "3 inches."

Reference Nos.:—1 L. 1, 2, 6, 9, 13, 18, 25, 32, 35, 36, 43: 2 L. 7, 12, 20, 37: 3 L. 11, 23: 4 L. 5, 14, 16: 1 M. 1, 2, 4, 8, 13, 17, 18, 22, 25, 28, 29, 32, 35, 36, 40, 45, 46, 48: 2 M. 3, 7, 10, 12, 15, 20, 27, 31, 33, 37, 39, 42, 50: 3 M. 11, 23, 38, 47: 4 M. 5, 14, 16, 19, 34, 41, 49: 1 S. 2, 4, 8, 17, 18, 22, 28, 30, 32, 36, 46: 2 S. 3, 10, 12, 15, 20, 26, 27, 31, 33, 37, 39, 42, 44, 50: 3 S. 21, 38, 47: 4 S. 16, 19, 24, 34, 49.

Secondary sex characters classified as previously.

The table shows that 15 per cent. of large birds, 17 per cent. of medium, and 15 per cent. of small often present sex differences. In this respect there is little difference, but of large birds 55 per cent., of medium-sized 43 per cent., of small 33 per cent. present no sex difference. Examination horizontally also shows that large birds less often present secondary sexual dimorphism than the medium-sized or small birds.

Instead of studying birds as a whole, certain families, chosen at random, have been examined by themselves with respect to the question of size. In barbets, jacamars, puff-birds, woodpeckers, and toucans the Tables III. and VIII. show that the smaller species present the most secondary sexual dimorphism. In hornbills and kingfishers, however, this association is not found, though the reverse does not hold.

Other families show the effect of size without any detailed analysis; for instance, in the Anatidæ swans and geese present little or no sex difference, and in the Falconidæ it is only the smaller species which show any sex difference.

On the whole, therefore, the consideration of size appears to support the thesis.

TABLE VIII.

		a.	v.s.l.d.	s.l.d.	so.d.	d.	v.d.
Barbets	No. of species	29	—	1	—	1	3
	Average total length	8.0	—	7.4	—	6.0	5.8
	No. of species	43	1	1	1	3	4
	Average wing-length	3.44	3.1	3.4	3.3	3.23	2.69
Jacamars	No. of species	1	8	5	1	—	—
	Average total length	11	8.2	7.7	8	—	—
Puff-birds	No. of species	8	—	2	—	—	—
	Average total length	7.5	—	7.0	—	—	—
Kingfishers	No. of species	13	2	7	11	1	1
	Average length	9.5	10.2	12.0	10.0	8.5	9.0
Woodpeckers.	No. of species	1	103	100	7	3	—
	Average length	24	27	22.6	19.7	21	—

NOTES.—Compiled from Monographs on the Capitonidæ by C. T. & G. L. Marshall; Galbulidæ and Buccconidæ by P. L. Sclater; Alcedinidæ by R. B. Sharpe; Picidæ by Alf. Malherbe.

For column headings, see Table III.

Sociability.—This is another factor which should protect birds from enemies to some extent. Numbers may be able to resist an enemy to which one would fall a victim. Sociable birds should, therefore, show less secondary sexual dimorphism—as is the case, see Table IX.

TABLE IX.

	Sociable Birds.	Not Sociable.
1	12	4
2	4	9
3	1	1
4	0	5

NOTES.—Compiled from F. Finn's 'The World's Birds.'

Of the remaining birds no note is made except Passerine birds, which are described as sometimes sociable.

Some birds form coveys or family associations out of the breeding-season—game-birds, for instance, and other birds form flocks, *e. g.* ducks.

Reference Nos. :—1 Soc. 1, 2, 4, 9, 18, 22, 25, 30, 35, 36, 43, 48 : 2 Soc. 7, 33, 42, 44 : 3 Soc. 47 : 1 Non-soc. 8, 28, 32, 45 : 2 Non-soc. 3, 10, 12, 20, 26, 27, 31, 39, 50 : 3 Non-soc. 21 : 4 Non-soc. 5, 16, 19, 24, 49.

Secondary sex characters classified as before.

Birds may also avoid enemies by having a habitat where they are free from enemies—for instance, mountain-tops, islands, arctic regions, oceans. Oceanic species are included in Table I. The only other material with which it has been found possible to examine this question is Seebohm's monograph of the Turdidæ ; for in this family there is a sufficient number of insular and continental forms for comparative purposes. Table X. sets out the material, and it can be seen that secondary sexual dimorphism is much less common in insular than in continental species. Of the four continental species of the genus *Merula* which present little secondary sexual dimorphism, it is noteworthy that there are three living high up on volcanic mountains.

TABLE X.

	<i>Insular.</i>						<i>Continental.</i>					
	a.	v.sld.	sld.	so.d.	d.	vd.	a.	v.sld.	sld.	so.d.	d.	v.d.
<i>Merula</i>	6	9	3	1	0	4	0	2	2	4	17	15
<i>Geocichla</i> ...	14	0	2	0	0	0	18	0	2	0	1	3
<i>Turdus</i>	8	—	—	—	—	—	36	—	6	—	2	—
<i>Mimocichla</i> ...	3	—	—	—	—	—	—	—	—	—	—	—

NOTE.—Compiled from H. Seebohm's 'Turdidæ.'

Endeavours were made to find other material in order to substantiate or not this remarkable correlation, but none was found suitable for classification.

Song, another secondary sexual character, was also treated in the same way, and clearly substantiates the former finding, as is shown in Table XI.

TABLE XI.

	<i>Insular.</i>			<i>Continental.</i>		
	Sing.	?	No song.	Sing.	?	No song.
<i>Merula</i>	5	18	3	17	21	1
<i>Geocichla</i>	2	13	1	9	14	1
<i>Turdus</i>	1	7	1	30	16	1

NOTE.—Compiled from H. Seebohm's 'Turdidæ.'

?=No note was made with reference to song. No song includes such descriptions as "song not known," "bird is silent," "never heard."

Birds may be looked at with advantage from another point of view. In Table XII. they are classified according to their sexual dimorphism without reference to any other factor. Examination of this table (XII.) shows that among birds presenting no sexual difference (column 1) 10/22nds 45 per cent. are relatively free from enemies; among birds usually presenting no sex difference (column 2) 5/15ths 33 per cent.; among birds sometimes presenting sex difference 2/5ths 40 per cent., and among birds usually presenting sex difference 0/8ths 0 per cent. are free from enemies.

TABLE XII.

1.		2.		3.		4.	
N.L.	L.	N.L.	L.	N.L.	L.	N.L.	L.
10	12	5	10	2	3	0	8
45 ⁰ / ₀		33 ⁰ / ₀		40 ⁰ / ₀		0 ⁰ / ₀	

NOTES.—Compiled from F. Finn's 'The World's Birds.'

Numbers at column headings refer to secondary sex characters as before. N.L.=not liable to attack; L. liable to attack; ⁰/₀=percentages of birds not especially liable to the attack of enemies. This is a synopsis of the previous table.

Reference Nos.:—1 N.L. 1, 2, 6, 13, 17, 18, 32, 35, 36, 43: 1 L. 4, 8, 9, 22, 25, 28, 29, 30, 40, 45, 46, 48: 2 N.L. 7, 12, 20, 33, 44: 2 L. 3, 10, 15, 26, 27, 31, 37, 39, 42, 50: 3 N.L. 23, 47: 3 L. 11, 21, 38: 4 L. 5, 14, 16, 19, 24, 34, 41, 49.

Thus it is clear that birds liable to attack more commonly present secondary sexual differences than birds not so liable to attack. If, instead of considering birds from a broad standpoint, a more detailed analysis is made, the same result is arrived at. In

the case of passerine birds, powerful species are only to be found amongst those showing no sex dimorphism, *e. g.*, crows, drongoes, shrikes. Swallows, which are aerial birds, present little or no sex dimorphism.

The classification of sexual dimorphism chosen for analysis refers almost entirely to sexual dimorphism of colour; nevertheless, it will be advantageous to consider briefly other secondary sexual differences—song and precopulatory displays.

As regards song, this character is frequently to be found in birds presenting no sex differences in colour and form, but which, nevertheless, do not appear to be especially free from the attack of enemies—for instance, among warblers, American warblers, wrens, cuckoos, larks, pigeons; whilst among birds not liable to attack, song-birds are very uncommon, if not entirely absent.

It thus appears that this dimorphic character is correlated to vulnerability to enemies, and accounts for some of those cases of birds presenting little or no sexual dimorphism of form or colour, but which are yet liable to the attack of enemies.

Precopulatory displays, or the displays of courtship, is another secondary sexual character open to investigation. Here, again, birds showing little or no display are birds not liable to attack, whereas birds showing great display are especially liable to attack. In the 'World's Birds,' under the heading "Courtship," sexual displays are briefly described in 25 of the 50 families under consideration. In the case of 19 of the 25 the usual actions are described: against diurnal birds of prey there is the remark "never seen the display," divers "said to be on the wing," hornbills "little known"; whilst against bustards "very elaborate," game-birds "elaborate," cranes "very elaborate." Cranes, then, form an exception, for they possess weapons of defence. Nevertheless, certain factors might lead one to suspect that they are not entirely free from attack; they are terrestrial birds, they are excellent-eating (their food being mostly vegetables, seeds, etc.), and in the East they are a favourite quarry of the hawk; they are also usually not sociable during the breeding-season, and, lastly, in most species both sexes take equal part in the displays, so that in truth they do not present secondary sexual dimorphism in this respect.

It is very fortunate that cranes needed this detailed consideration at the end of the examination, which has covered a great deal of material, as it is easy to draw attention to the fact that this is almost the only occasion (ducks also) when such treatment became necessary.

Summing up, it may be said that for certain reasons—namely, because of aerial, aquatic, and oceanic habits, possession of defensive and offensive weapons, of diving-habits, of ill-flavour to man, of large size, of insular habitat, of social disposition, of carnivorous habits—certain birds must be relatively free from the attacks of enemies; and it has been shown that these birds present less secondary sexual dimorphism than birds which for

other reasons—namely, possession of terrestrial and arboreal habits, of no defensive weapons, of non-diving habits, of no ill-flavour to man, of small size, of continental habitat, of solitary disposition, and of non-carnivorous habits—have been considered to be relatively liable to the attack of enemies. These two factors thus appear to be correlated, but it is obvious that, though great sexual dimorphism is only to be found amongst birds liable to attack, nevertheless the converse does not hold, for some birds which do not appear to possess any special characters which would protect them from attack, none the less fail to present any secondary sexual dimorphism, *e.g.* ibises, mound-birds, mouse-birds, rollers, barbets, and coursers.

Conclusions may be briefly stated :—

- (1) Among birds specially liable to the attack of enemies, secondary sexual dimorphism is chiefly to be observed.
- (2) Among birds not specially liable to attack of enemies, secondary sexual dimorphism is rarely found.
- (3) In both cases, birds presenting no sexual differences are represented, but much more commonly in birds more or less free from attack of enemies.

Having come to these conclusions, it will not be out of place to examine briefly the more important theories put forward to account for secondary sexual dimorphism, in order to discover whether any of them be substantiated or not.

Exuberance of Vital Energy in Males.—Wallace, in ‘Tropical Nature,’ believed that natural selection could account for secondary sexual dimorphism, by supposing that only the strongest and most virile males gained mates, and that these mates thus came to possess an excess of vital energy which became manifest in bright plumes, etc. If this be so, it is difficult to see the reason why birds vulnerable to enemies should be specially picked out. One would think that it would be dangerous for these birds to make themselves thus conspicuous, and would have anticipated that birds not liable to attack could have done so with more impunity.

Sexual Selection (Darwin, ‘Descent of Man’).—The argument used above applies similarly against Darwin’s theory, which in no way can account for the correlation under examination. One would have thought that female selection would have had freer play among birds more or less free from enemies than among birds frequently subject to their attack.

Nesting-Habits Theory (Wallace and others).—It has been noted that birds liable to the attack of enemies, and making open nests, more frequently present secondary sexual dimorphism than birds making closed nests. If, however, birds liable to the attack of enemies more often present secondary sexual dimorphism than birds in general, then it follows that birds making open nests, and also liable to the attack of enemies, must do likewise.

It is thus obviously necessary to decide which is the more

important correlating factor—vulnerability to enemies or open-nesting habits. Table XIII. deals with birds making open nests and in no way helps to decide the point; coursers, ibises, mouse-birds, tinamous, touracous, pigeons, rails, shore-birds, according to the “nesting-habit hypothesis,” should present sex dimorphism, but they also fail to fall into line with the other correlation.

TABLE XIII. (Open-nesting birds.)

Not especially liable to attack.	Liable to attack.
1. American Vultures, Cassowaries, Cranes, Divers, Grebes, Gulls, Storks, Penguins. 8	Coursers, Ibises, Mouse-birds, Tina- mous, Touracous. 5
2. Cormorants, Birds of Prey, Herons, Nightjars? 4	Pigeons, Rails, Shore-birds. 3
3. —	Curassows. 1
4. —	Bustards, Game-birds, Humming- birds, Sand-Grouse. 4

If, however, one turns to closed-nesting birds (Table XIV.), it is at once obvious that open-nesting habit plays no part, because several of the groups present considerable secondary sexual dimorphism, and quite a large number a small amount.

TABLE XIV. (Closed-nesting birds.)

1. Bee-Eaters, Hoopoes, Rollers, Motmots. 4
2. Barbets, Jacamars, Kingfishers, Parrots, Woodpeckers. 5
3. Hornbills, Toucans. 2
4. Trogons. 1

NOTE.—Compiled from F. Finn's 'The World's Birds.'

Table XV. continues the two previous tables, and also deals with families of birds making both open and closed nests. It shows that the relation between open-nesting habits and secondary sexual dimorphism is, if not entirely negligible, at any rate not nearly so close as with vulnerability to enemies. It may be

mentioned that the Australian warblers (Maluridae) present great sex difference (the males are amongst the most brilliant of birds), and yet they make closed nests. They are small defenceless birds, and so they not only form exceptions to the open-nesting theory, but support the correlation under consideration.

TABLE XV. (Nesting-habits.)

	Open nests.	Open and closed nests.	Closed nests.
1.....	13 65% 52% ₀	3 15% 33% ₀	4 20% 33% ₀
2.....	7 47% 28% ₀	3 20% 33% ₀	5 33% 42% ₀
3.....	1 33% 4% ₀	—	2 66% 17% ₀
4.....	4 50% 16% ₀	3 37% 33% ₀	1 13% 8% ₀

NOTES.—Compiled from F. Finn's 'The World's Birds.'

Honey-guides, parasitic; the rest, nesting-habits not mentioned.

Reference Nos. to middle column, the others are to be seen in Tables XIII. and XIV. 1 open and closed, 2, 32, 36; 2 open and closed, 10, 15, 44; 4 open and closed, 14, 19, 34. Percentages to right of figures = horizontal percentages, percentages below = vertical percentages.

Further, it is noteworthy that Honey-guides (Indicatoriæ) sometimes present sexual differences (Finn), and yet these birds are parasitic. This exception is important because it shows that the rearing of young as well as the open-nesting habits cannot account—in this case, at any rate—for secondary sexual dimorphism.

The Aphrodisiac Theory.—Those who believe in the necessity for an aphrodisiac (bright feathers, sexual display, and song) must assume coyness on the part of the female. Little, if any, attempt, however, is made to establish this important sexual difference—a coy female and an impudent male. There does not appear to be any reason why the females of birds especially subject to the attack of enemies should be especially coy, or that among birds not especially subject to attack the females should not require a powerful stimulant.

The Catabolism Theory (Prof. Geddes and Thomson, 'Evolution of Sex,' 1889).—The secondary sexual structures found in the males are considered to be due to a katabolic constitution, and their absence in the female due to an anabolic tendency.

No attempt is made to explain the distribution of secondary sexual characters among birds on this theory, or to give a reason

why some birds present great extra-sexual difference and others little or none. The conclusions arrived at in this paper do not appear to be explicable on this theory; there seems to be no reason, for instance, why birds especially subject to the attack of enemies should be more katabolic than birds not especially so subject.

The Mendelian Theories.—Although the followers of Mendel have carried out very important investigations with regard to secondary sexual characters, as far as I am aware, they have made no attempt to account for the distribution of these characters in the animal kingdom.

The Hormone Theory ('Archiv für Entwicklungsmechanik,' 1908), J. T. Cunningham.—According to this theory, secondary sexual characters become established in the following manner:—As a result of certain mechanical and functional stimuli, confined, for instance, to the male, certain organs of the male take on new characters: these are acquired characters. During their production a specific hormone is produced, which stimulates the corresponding determinant in the gametes and alters them in such fashion that, during development, they reproduce the acquired character; but it also alters them in another direction—it implants in them an ability to reproduce the acquired character only in the presence of the male sexual hormone. In the absence of the male sexual hormone, the character cannot develop: for instance, if a stag be castrated the antlers cannot develop on account of the absence of the male hormone—the character remains dormant. Obviously the material here dealt with applies only to the first part of the theory, that dealing with mechanical and functional stimuli.

In the case of birds the functional stimuli, which call forth the bright plumes of the males, are those associated with the display of these ornaments during courtship, "the tail of the peacock became brilliant and hypertrophied because it had been constantly erected." The stimulus calling upon the male to display seems, therefore, to be the deciding factor. Thus in order to support this theory, it would be necessary to show that the males of birds subject to enemies suffer more from such stimuli than do those birds relatively not liable to be attacked.

Finally, it is necessary to point to the importance of the correlation under consideration with respect to the possibility of it being able to account for the presence of secondary sexual characters.

The activities of animals fall under three headings:—

- (1) Those associated with the procuring of food.
- (2) " " " " escape from enemies.
- (3) " " " " reproduction.

It has usually been thought that the sexes bear the same relation to the environment as regards the procuring of food and the escape from enemies; and therefore to account for secondary

sexual characters, search has always been made in the reproductive environment. But the correlation between secondary sexual dimorphism and vulnerability to enemies indicates that a solution to the problem may possibly be found to be related to the activities associated with the escape from enemies, and especially if it could be shown that the sexes do not bear the same relation to the environment as regards escape from enemies.

The author has attempted to show elsewhere ('Controlled Natural Selection,' 1914) the lines along which solution may possibly lie.

Reference List of Birds.

- | | |
|------------------------------------|----------------------------------|
| 1. American Vultures (Cathartidæ). | 26. Jacamars (Galbulidæ). |
| 2. Auks (Alcidæ). | 27. Kingfishers (Alcedinidæ). |
| 3. Barbets (Capitonidæ). | 28. Motmots (Momotidæ). |
| 4. Bee-eaters (Meropidæ). | 29. Mound-birds (Megapodiidæ). |
| 5. Bustards (Otididæ). | 30. Mouse-birds (Coliidæ). |
| 6. Cassowaries (Casuariidæ). | 31. Nightjars (Caprimulgidæ). |
| 7. Cormorants (Phalacrocoracidæ). | 32. Owls (Strigidæ). |
| 8. Coursers (Glareolidæ). | 33. Parrots (Psittacidæ). |
| 9. Cranes (Gruidæ). | 34. Passerine Birds (Passeridæ). |
| 10. Cuckoos (Cuculidæ). | 35. Penguins (Spheniscidæ). |
| 11. Curassows (Cracidæ). | 36. Petrels (Procellariidæ). |
| 12. Birds of Prey (Falconidæ). | 37. Pigeons (Columbidæ). |
| 13. Divers (Colymbidæ). | 38. Puff-birds (Bucconidæ). |
| 14. Ducks (Anatidæ). | 39. Rails (Rallidæ). |
| 15. Frogmouths (Podargidæ). | 40. Rollers (Coraciidæ). |
| 16. Game-birds (Phasianidæ). | 41. Sand-Grouse (Petroclidæ). |
| 17. Grebes (Podicipedidæ). | 42. Shore-birds (Charadriidæ). |
| 18. Gulls (Laridæ). | 43. Storks (Ciconiidæ). |
| 19. Hemipodes (Turnicidæ). | 44. Swifts (Cypselidæ). |
| 20. Herons (Ardeidæ). | 45. Thick-knees (Edicnemidæ). |
| 21. Honey-guides (Indicatoridæ). | 46. Tinamous (Tinamidæ). |
| 22. Hoopoes (Upupidæ). | 47. Toucans (Rhamphastidæ). |
| 23. Hornbills (Bucerotidæ). | 48. Touracous (Musophagidæ). |
| 24. Humming-birds (Trochilidæ). | 49. Trogons (Trogonidæ). |
| 25. Ibises (Ibididæ). | 50. Woodpeckers (Picidæ). |